A COMPARISON OF THE RESPONSES OF SESSILE AND MOTILE PLANTS AND ANIMALS

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I. INTRODUCTION

D<small>URING</small> the past few years the attention of biologists
has turned more and more from those phenomena which
were supposed to be comparatively fixed, to responses to
stimuli.   Physiologists have long been concerned with
the mechanism of response; psychologists are interested
in its modification.   Geographers, climatologists and
ecologists have recently turned their attention to re-
sponses in natural environments and zoologists have
become interested in response, particularly from the point
of view of its specificity.   In these quite independent
investigations and compilations there has been little
attempt at analysis with a view to determine legitimate
lines of comparison among the exceedingly diversified
types of organisms which have been investigated, and
some confusion has resulted.   For example, since the
more obvious responses of plants are structural, persons
not familiar with comparable phenomena among animals
have made erroneous comparisons of sessile plants and
motile animals.   This paper is written to present in as
nearly uniform terms as practicable (*a*) analysis of kinds
or aspects of response, (*b*) justifiable kinds of compari-
son, and (*c*) the bearing of response phenomena on
biological theory and controversy.   It aims to show that
the numerous kinds of response are reducible to a few
simple types common to both plants and animals, and that
the failure to consider all types has been responsible for
confusion and various one sided theories.   It further aims
to show that study of response during the past few years
has led to an unusual broadening of our conceptions.

II. BASIS OF DISCUSSION

As a basis for discussion we must first have a clear
understanding of the character and definition of response.
Secondly, we must determine what constitutes an indi-
vidual in those plants and animals that are made up of
repetitions of parts.   Thirdly, we must note whether or
not the organism is sessile or motile, capable of playing
the part of either, or colonial pelagic.

1. Responses

The word response is used in various slightly different senses. In general it refers to more complex and time-requiring phenomena than "reaction." In geography the term has been used (Goode, '04) to cover all changes in culture supposed to be produced by climate or other geographic conditions. It is also applied by geographers and geologists to changes in the physical characteristics of man (evolution) which Goode ('04) has stated are slower than the cultural responses. In general botanists have used the term to cover changes of plant structure and function induced by external conditions. Cowles ('11), however, uses the word "reaction" to cover these phenomena. Coulter ('09) used the term response as synonymous with adaptation in plants. Zoologists have used the term to apply to changes in animals due to external conditions, but with little agreement as to what is to be included. We will use it *here* to include *reactions, changes in functions, structure, color, induced by external* conditions either directly or indirectly, without regard to how simple or how complex the processes involved may be.[1] The length of time required to bring the changes about may arbitrarily be taken as not exceeding the time required to breed five to ten generations of the species concerned. All organisms respond to stimuli because each stimulus acts upon some internal process. Strictly speaking, the response is the *change or changes in the physical or chemical processes of the organism (or the part or parts concerned) which results from the disturbance.*

Those things which we commonly see and term response are often the *later* and *less important* phases of the disturbance. The striking phases of responses of motile organisms are usually movements which follow closely upon stimulation. In sessile organisms the noticeable responses often appear only after a considerable period. In both sessile and motile organisms some responses are

[1] For good representative bibliography see Adams, '13, Ch. VIII and IX.

not evident because they concern internal, chemical and physical processes which affect neither form nor movement. Changes in the enzymes secreted by digestive glands, which accompany changes in food (Jennings, '06, p. 347), are examples. While thus recognizing that responses are concerned primarily with internal processes, we must of necessity refer chiefly to the external phases.

2. Sessile and Motile Organisms

Sessile organisms are those which are sedentary in habit, whether attached or possessing slight powers of locomotion. Motile organisms are those that habitually move about. Vagile or creeping forms as well as swimming, walking, flying, burrowing types are included. Most sessile animals are capable of moving their parts, while only a few sessile plants possess this capacity, and these only to a slight degree.

There is no sharp distinction between sessile (sedentary) and motile organisms. Every possible gradation exists between fixed non-motile types as *trees* on the one hand and the *pelagic fishes* on the other. It is the extremes which we will compare.

3. The Individual and Its Relations in Colonies and Groups

The following comparison of animals and plants is an attempt to distinguish potential or incomplete individuals in colonial organisms and compound organisms which, while not commonly recognized as colonial, are made up of incomplete individuals.

(a) Animals and Plants made up of Single Individuals

The vast majority of animals belong here. Most protozoa, solitary sponges, solitary hydroids, sea anemones, worms not preparing for asexual division, echinoderms, mollusks, arthropods and vertebrates. Only single-celled plants, young seedlings and possibly a few adults of multicellular plants which *possess* but *one growing point*

(exclusive of roots) belong in this group. *Single individuals* as described here are the basis for determining what shall be called individuals in *colonial* and *compound* types.

(b) Colonial or Multiple Individualed Plants and Animals

A number of animals and the vast majority of the plants belong here. The group can be roughly divided into two types, (*a*) those having a chain or plate arrangement of incomplete individuals and (*b*) those having a branching or tree-like arrangement. The groups of incomplete individuals of type *a* occur among the Protozoa, worms undergoing asexual reproduction, many of the Bryozoa and some of the Tunicates; both sessile and pelagic (plankton) forms occur. On the plant side type *a* includes plate-like colonies of algæ, filamentous algæ, some thallose plants and probably some of the fungi, though the great multiplicity of forms makes the separation of this group from the branching tree-like types, difficult.

Type *b* includes some of the colonial Protozoa, the majority of the sponges, hydroids, corals and the branching Bryozoa. The algæ, fungi, mosses, ferns and flowering plants are all represented. The colonies are usually attached to the substratum (sessile).

i. *Numbers of Individuals.*—Among the animals the number of so-called *zooids* is the number of incomplete *individuals*. In the sponges there are as many zooids as there are *excurrent openings* (osculæ) (Minchins, '00, p. 91). Zooids usually possess a mouth opening and organs for securing food, though in some cases they may be specialized for reproduction, defence or locomotion as in some of the Cœlenterates. Among the colonial plants there are as many incomplete individuals as there are *buds* or *growing points* (vegetative regions). There are no regularly occurring organs in animals, strictly comparable to leaves. However, any organs such as tentacles, gills, etc., which secure or absorb nutriment may be re-

garded as *analogous* to leaves. *Each potential bud with its leaf may be compared to a zooid.* In comparing plants and animals, *roots can perhaps be compared with the holdfast organs of hydroids.* In both groups, roots and root-like organs are individuals of a very *low order of individualization* and of a type not well represented among animals. The holdfast organs of animals are not important absorbers of food and water.

ii. *Stems and Other Connecting Organs* (*Conducting Tissues*).—The most striking difference between the incomplete individualed or colonial plants and colonial animals is the presence in the former of specialized stems and highly complex conducting tissues (Cowles, '11; Pütter, '11, pp. 361–66). The conduction of food materials from the root to other parts of the plant and from the leaves to the root is a functional necessity not paralleled even in those colonial animals showing the greatest division of labor. In animals stems are relatively undifferentiated and are often made up of living, relatively unspecialized zooids, as, for example, in many *Bryozoa* such as *Crisis*. The tendency to cauliflory in some plants and the ability of cambium to produce shoots and of the stems of most hydroids to produce individuals indicates that such a condition may be potentially present in all. In stalked *Protozoa* the stems are solid, while in most Cœlenterates they are tubes, usually simple though sometimes complex, made up by mere elongation and branching of the stock of the simple single forms such as the *Hydra*. The lumen is usually ciliated and makes possible a transfer of material which renders practicable such division of labor as occurs in this group (Pütter, '11). In the *Bryozoa* the different zooids have their body cavities joined in the simpler forms merely as a branching lumen of the main wall of the colony; in others by small openings the more specialized of which are sieve-like plates (Harmer, '01, pp. 471 and 496; Delage and Herouard, '97, Vol. 5, p. 62).

The connection between the individuals of the tunicate colonies is often very complex, due to the fact that in the

most complex types the stolon (stem) gives rise to new individuals and possesses all the layers of cells which take part in forming them. The connection between different individuals differs in different groups and is determined by the particular mode of asexual reproduction. As the individuals are quite independent of one another in function, these connections do not have the same significance as in plants. Even where there is a common blood circulation, as for example in the *Clavellinidæ* (Harmer, '04, p. 71), there is no noteworthy division of labor.

iii. *Metabolic and Reproductive Relations of Individuals.*—The flat worms at certain times consist of chains of zooids at various stages of development and with various degrees of independence. Child ('13) has found that these chains of zooids present a series of gradients in rate of metabolic reaction. The rate is highest at the anterior end of the whole chain and decreases toward the posterior end, not uniformly, however, for the rate is *lower* immediately in front of each head region than it is in the head region itself. A gradient is present in the axis of each zooid. The most anterior head dominates so long as the chain remains intact. In the corals certain zooids dominate (Wood-Jones, '11) over the others. Some types have a single dominant zooid and some more, while in other cases all are equal.

Among plants whose form is that of a chain or a plate the individuals are less closely bound together and dominant vegetative regions are probably less well developed. In the branching types, dominant vegetative regions occur (Cowles, ''11, p. 747; Goebel, '00, Vol. I, p. 206). In the conifers, for example, there is a leader, a dominant growing region at the tip of the main stem just as in certain madrepore corals (Wood-Jones, p. 83). Other plants like the elm have *several* vegetative regions which dominate over others, as they do in the branching madrepores.

Growth form or colony form varies according to certain laws dependent, in part at least, upon the metabolic

relations of individuals. Thus Wood-Jones says of the corals—

a colony may grow according to five different types of vegetative growth . . . it may grow as (1) a spherical mass, (2) an encrusting layer, (3) a free plate, (4) a branching tree-like growth, or (5) a mere amorphous lump.

He further notes the division of all the corals into two groups of normal growth-forms; for *all the zooids may take an equal share* in the asexual reproduction or, again, *some may be of greater importance than others,* and the asexual reproductive functions may be lodged in a very few individuals only. Considering the first division (all zooids taking equal share, the principal types of budding vary from each other in the actual site of origin of the daughter zooid from the parent, in the degree of final separation of the two zooids, and in the thickess of the intervening partition between the two zooids. The amount of rising above the general surface by each individual zooid is likewise subject to variation.

Turning now to the corals that constitute the second class (some zooids of greater importance than others) which in the words of Wood-Jones have some of their units specialized as active agents of growth,

it is at once seen that the possibilities of variation of normal vegetative habit are greatly increased. All the elaborate branching forms, plates and leaf-like growths belong to this class; and all are evolved by special peculiarities of the growing point. The zooids that constitute the growing point may take various forms; they may be arranged as a cluster, as a creeping edge, or as many varieties of terminal shoots of branches.

In the first instance, it is necessary to draw very sharp distinctions between two subdivisions of this group. In *Group 1* come all those forms like *Montipora,* whose distal zooids are the newest formed members of the colony; and in *Group 2* are included the *Madrepora,* whose distal zooid is the most ancient individual in the whole group.

In dealing with *Group 1* many forms have to be considered, for when the youngest are the active zooids their growth cluster may be variously disposed, and on its disposition the resulting vegetative form entirely depends.

In *Group 2,* however, this state of things is entirely altered, for there one zooid, which is situated at the extremity of the stem, and which I

shall call throughout the "*dominant apical zooid*," constitutes the growing point; and this zooid is the parent of the entire colony.

Various writers make comparable statements or show comparable principles among hydroids (Motz-Kossowska, '08) and Bryozoa (Davenport, '91, et al.) and among plants (Goebel, '00). Of the colony form of the tunicates Herdman ('04, p. 82) says:

The marked differences in the appearance of the colonies of compound Ascidians is largely due to the methods of budding; even in those of stolon type where the budding is practically the same in essential nature, the results may be different in superficial appearance, according as the buds are formed on a short stolon close to the parent body, or from the extremity of the post abdomen or from the long epicardiac tube which may extend for some inches from the ascidiozooid.

Thus we conclude that the innate causes of different growth-forms (colony forms) of colonial organisms are (*a*) the *mode of division of the zooids* or vegetative regions, (*b*) the *ratio of stem elongation to number of zooids* or buds produced or uniformity or lack of *uniformity of stem elongation* (Wood-Jones, p. 76) closely related to (*c*) the presence or absence, *number, position* and *region* of influence of the *dominant growing* regions or dominant zooids, and (*d*), in some cases, the *grand period of growth* and the *length period of the internodes* (Johnson, '11). The innate tendencies are thus reducible to a few principles applicable to both plants and animals.

(*c*) *Responses of Motile Organisms*

i. *Movements.*—In motile organisms the most striking responses are changes in position brought about by movements usually more or less random, and which bring the organism into various conditions one of which usually relieves the disturbance. The organism resumes normal activity in conditions which brought the relief (Jennings, '06). These conditions are not necessarily advantageous, but are usually so when the stimuli are those encountered in nature (Mast, '11). Behavior of motile organisms is also modified by repetition of action even in animals as low in the animal series as the *Protozoa* (Holmes, '11).

Jennings ('06) has quoted various botanical workers'
observations on motile plants the behavior of which prob-
ably follows the general laws governing the behavior of
motile animals. As a result of the quick behavior re-
sponses of motile organisms, their distribution at any
given time is a better index of the conditions at that time
than the distribution of sessile organisms, because when
the conditions at a given point become unfavorable the
motile organisms usually move to another situation,
while the sessile forms remain and perhaps die.

ii. *Structural Responses.*—Among motile animals,
structural and color changes occurring as a response to
environmental conditions (stimuli) are usually not of
importance to the organism concerned. The color differ-
ences induced in *Lepidoptera* by heat and cold (Stanfuss;
Fischer) and the structural differences in Crustacea such
as were brought about in *Cladocera* by Woltereck, and
other modifications brought forward recently, are usually
of no known advantage or disadvantage to the animals
concerned (Bateson, '13, Ch. IX and X). Such re-
sponses in color and general form do not ordinarily take
place in adults subjected to such conditions. The strik-
ing structural responses of motile animals are often
responses to the organism's activity. The use and disuse
phenomena of the Lamarckians, the increase in size and
form of muscles, thickening of skin in man and mammals,
are well-known examples of a type of responses which
have influenced zoological speculation. Child ('04) con-
trolled the form of *Leptoplana* by controlling activity.
Holmes ('07) found that the movements of pieces of
Loxophyllum have an important part in shaping the
general outline of the bodies of the resulting forms. The
general forms of motile animals are correlated with their
activities but whether form or structure correlated with
it appeared first in the course of evolution has been the
subject of considerable fruitless speculation.

(d) *Responses of Sessile Organisms*

i. *Structural Responses.*—The striking phases of responses among colonial sessile organisms are often changes in form and structure, or the relative position of the parts. The changes in structure or position of parts are not necessarily advantageous or useful, but are usually so when the stimuli are those commonly encountered in nature (Cowles, '11; Loeb, '06, p. 124; Wood-Jones, '11; Ch. VIII). Indifferent and detrimental responses are often given under experimental conditions and no doubt the absence of such variants among sessile animals collected in a wild state is due in part to the failure of such organisms to survive. A few sessile colonial organisms such as cacti (Cowles, '11) show little or no plasticity.

Among sessile animals, the observations of Wood-Jones form the best examples of response. He found that the branching type of corals dominated in barrier pools, tall slender non-branching types in deep water, and massive boulder types on surf beaten shores. Thus he figures similar colonies of *each of three genera* which, while possessing certain peculiarities of their own, are in general agreement as to *growth form* just as sessile plants usually are; and this in part for comparable reasons. Thus various conifers occur as *Krummholz* in the high mountains, due to severe conditions (Cowles, '11, p. 732), wind, snow, and in part to the injury of *terminal growth regions* of the main stem which gives rise to lateral branches. The boulder-like corals with the zooid at the same level occurring on the surf-beaten shores of coral islands are due, in the case of Madrepora, for example, to repeated injury of the *terminal dominant zooids.* Conifers in protected situations often grow into *tall slender trees* comparable with the (deep) *still-water corals.* The barrier pools afford conditions where the terminal buds are less often injured than in the surf and the tree-like branching corals result from minor injuries to dominant zooids.

Wood-Jones finds further that still-water corals are less strongly calcified than those in rough water, the strains producing increased secretion analogous to increased tissue production as a result of mechanical strains in plants (Cowles, p. 669). Corals show different kinds of growth under different environments particularly when injured. The new part may be different from the rest and adjusted to the environment thus making it appear as though two "species" occurred in the same colony. The mode of division of the zooid is also different under different conditions. Plants show similar variation with changes of conditions, particularly in the leaves which are *divided* in submerged portions of amphibious plants and entire in the emerging portions (Cowles, '11, p. 595).

As has been noted, there is nothing in sessile animals that is more than roughly analogous to leaves. Leaves show marked structural differences on different parts of the same tree where the environmental conditions are different, as, for example, in the differences which occur between the upper and lower portions of a forest tree. While there are, no doubt, differences in similar details (histology) in the organs of display in different parts of the same colony of sessile animals, little or nothing has been done upon them. As a further indication of the prevalence of structural response in sessile organisms of the hydroids Hickson states that there is probably but one species of *Millepora* which occurs in a large number of growth forms. The commercial sponges (Moore, '08) and common freshwater sponges and polyzoa show many different forms under different environmental conditions.

The major differences in growth form induced by external stimuli in colonial organisms result from modifications of the rate and character of growth with respect to the *four innate* tendencies toward various growth or colony forms discussed above, and which may be briefly enumerated as follows: (*a*) mode of division, (*b*) amount of stem elongation, (*c*) influence of dominant regions and

(*d*) grand period of growth and the length of period of internodes.

The principles are concerned with asexual reproduction and apply to motile organisms only exceptionally as for example in the case of colonial pelagic forms. The laws are applicable to both plants and animals.

ii. *Movements.*—Movements of sessile animals are usually contractions or extensions of parts or of the entire body. Tentacles and comparable organs are capable of movements for securing prey. Such organs often tend to wrap about objects which are in motion. Many sessile animals are capable of opening and closing a mouth opening and of bending or twisting the entire body. Plants possess a comparable capacity only occasionally.

(*e*) *Behavior of Sessile Motile Organisms*

Most sessile animals are capable of some movement and react by contraction of parts. The reactions may be modified by repeated stimulation (Jennings, '06) and usually by physical factors. Some animals, as *Hydra, Stentor* and many others are both sessile and vagile or free-swimming, and show different types of behavior when attached and when free. Jennings states that such protozoa have a more complex behavior than motile forms. This is due to their combining the types of behavior of sessile and motile animals.

(*f*) *Response and Taxonomy of Sessile Organisms*

Hickson ('98) has stated that there is but one species of *Millepore* and believes that sex organs will be found to be the best taxonomic characters. Wood-Jones states that there are far fewer species of corals than has formerly been supposed, and states further that growth form can not be used to distinguish species. Among fresh-water sponges and Bryozoa reproductive bodies (*gemmules* and *statoblasts*) have been found to possess satisfactory taxonomic characters. This is a situation quite parallel with that in plants where reproductive

organs are used as classification characters. The ideas of the reproductive organs of plants are now at the "fixity" stage which on the animal side is paralleled by the idea of fixed tropisms and fixed instincts, of a few years since. Variability of tropisms is now well recognized and reproductive organs in plants are being found plastic, as those of animals will probably be found also.

III. PARALLELISM BETWEEN SESSILE AND MOTILE ORGANISMS WITH REFERENCE TO ECOLOGY

From a summary of the considerations above it will be seen that for practical comparison the *division of organisms into plants and animals may be abandoned and only reference to sessile and motile organisms made*. We may now turn to a discussion of a few general principles making the division into sessile and motile organisms only. The behavior of motile organisms is plastic. There are innumerable cases of modification of reaction by variations of physical factors (Jennings, '06; Loeb, '06; Mast, '11). If for purposes of discussion we put the usual "normal" reactions of motile animals over against "normal" structure of sessile animals, we note that the *behavior response* of the former *parallels* the *structural response* of the latter.

1. Breeding

Motile Organism

(a) The breeding activities take place within narrower limits than any other activities. Merriam, '90; Herrick, '02; Reighard, '08; Shelford, '11a, b, c, '12a, b.

(b) The selection of breeding place and breeding activities, including first activities of the young, are governed by the same general laws as other activities.

Fixed (Sessile) Organisms

(a) Breeding and other activities within same limits, except that dispersal may take place over wide areas through detachability of seeds and other reproductive bodies.

(b) Less marked because a selection of abode by sessile organisms takes place through the behavior of motile young stages or through wide dissemination of non-motile bodies by wind (etc.) with growth under favorable conditions and failure elsewhere.

(*c*) The breeding activities are probably least modifiable and least regulatory.

(*c*) The reproductive organs and early embryonic stages are less modifiable than the vegetative parts.

(*a, b, c*) The maple tree, a sessile organism, is entirely stationary in its adult stages. The seeds are blown by the wind. One would not accomplish much in the study of ecology by studying the distribution of the seeds of the maple, or, on the other hand, by the study of the distribution of adult birds, without some further discrimination.

Sessile organisms are not difficult to associate with their proper environmental conditions in their adult stages. As we proceed in our study to forms which can move readily and rapidly, the difficulty of associating them with their definite environmental conditions increases. Sessile organisms have stages which are small and capable of easy dispersal, as in the case of the maple. Sessile marine animals and some sessile plants frequently have motile forms in young stages. In these motile stages they are governed by the same laws as other motile organisms. The conditions under which the motile stages develop into the sessile forms are crucial.

Most fresh-water forms and some marine forms of sessile organisms are without the free-swimming stage, and they produce non-motile stages physiologically comparable to the seeds of higher plants. The winter bodies (statoblasts) of the Bryozoan (*Pectinatella*) common near Chicago, and which is a strictly sessile organism, are comparable to seeds and probably require "ripening" by cold, just as do many seeds and the reproductive bodies of some other species of the same group. Organisms which are highly motile in the adult stages are not motile in the egg and young stages. The eggs and young of birds, for example, do not move about, yet birds are the most motile of all animals.

2. Comparison of the Sessile and Motile Elements of the Biota

(*a*) The motile organisms of a given habitat usually react simi-

(*a*) The sessile organisms of a given habitat (particularly plants)

larly to two or more stimuli not differing greatly in intensity from their optimum, *i. e.*, the percentage of positive or negative trials is essentially the same for standard intensities. There is also probably similarity in the rates of metabolism, etc.

usually show similar functional rates, such as similar rates of transpiration among sand dune plants.

(*b*) The *specificities* of *behavior* such as the mode of *moving* the organs, *e. g.*, of locomotion, and in some cases the combined results of *different behavior reactions* are similar and hence are *ecologically* equivalent. The size and efficiency of the organs are also involved.

(*b*) The various structural devices which meet the conditions of the environment are ecologically equivalent.

A testing, for example, of the rheotaxis of a large number of brook-rapids animals has shown them to be strongly positive, and when active individuals only are considered the percentage of positive trials is very similar for the entire rapids community. Likewise they are in accord in their avoidance of sand bottom. Many of the animals have special means of attachment which may be brought into play with speed.

As has already been pointed out elsewhere, ecological equivalence is illustrated here. The darters (fish) are strong swimmers and are able to live in rapids by virtue of their swimming powers and positive reaction, while snails meet the same general conditions through positive rheotaxis and the strong foot which enables them to hold to rocks.

3. Sessile and Motile Organisms in Ecological Succession

(*a*) Ecological succession is succession of ecological (physiological) types over a given area, due to changes of conditions which both cause migration of physiological types and transformation of such types as remain (Shelford, '11*a*, '11*b*, '11*d*, '12*a*, '12*b* and citations). Changes of conditions are geographic, *i. e.*, physiographic, climatic,

etc., and biological (due to organisms). Sessile plants
are the chief biological cause of succession on land and
in fresh water, while sessile animals are the chief biolog-
ical cause in the shallow portions of the sea, especially in
coral reef regions (Wood-Jones, '11). Sessile organisms
are more important causes of succession than motile ones
because they (*a*) build up the substratum with detritus
and skeletons, (*b*) interfere with the movement of the
surrounding medium, (*c*) cut off light from the sub-
stratum where other organisms must reside and their
own young secure foothold, and (*d*) they usually affect
their own environments with excretory products more
than do motile organisms. In general we recognize
ecological succession of motile animals through the differ-
ences of behavior which accompany changes in conditions.
The differences are physiological; differences in behavior
are the easiest index of the physiological condition. The
character of nests, burrows, etc., are often good indi-
cators also.

IV. INFLUENCE OF RESPONSE PHENOMENA UPON BIOLOGICAL THEORY AND CONTROVERSY

A glance at some aspects of biological speculation
since before the publication of Darwin's "Origin of
Species" is essential to our understanding of the atti-
tude of biologists until recently, toward responses.

1. TELEOLOGICAL VIEW

In the matter of animal behavior response, the earlier
workers interpreted the reactions as intelligent and pur-
poseful, ascribing human sensations, etc., to animals as
low in the scale as protozoa. This teleological tendency
was paralleled on the plant side by the idea of purposeful
adaptive responses. Many common plants respond
(structurally) readily to environmental conditions. As
has been noted, the commonest of the surviving responses
of the wild state are apparently advantageous. This led
some botanists to a Lamarckian teleological conception of
response, perhaps best represented by Kerner and

Oliver's work on the natural history of plants. According to this view, responses are advantageous and for the *purpose* of *preserving* the plant. Thus response and adaptation become synonymous (Coulter, '08), a usage quite inapplicable to animal structure. At the beginning of the recognition of the response phenomena of corals Wood-Jones takes essentially the view of adaptation which botanists have tried and rejected.

Lamarck, who was for many years engaged in botanical work, must have noted many cases of advantageous structural response in plants. Later he undertook the study of invertebrates which show great plasticity, and was naturally much influenced in the development of his theory of transmutation of species by the response phenomena in the plastic organisms which he studied. Thus the responses of motile (as well as sessile) organisms which result from their own activities or the action of their environments formed an important feature of Lamarck's (Packard, '01; Cope, '96) theory of transmutation of animal species. His theory is clearly in accord with the material he studied most. The nature of his contention and various well-known circumstances caused his ideas not to be accepted.

2. NATURAL SELECTION VIEW

Characters used in classification of motile animals before and since the time of Darwin are quite frequently adaptation characters. Thus the large pectoral fins and absence of an air bladder are characteristics of an entire group of fishes, the darters. The divided eyes of the *Gyrinidæ,* which swim at the surface of the water, are so adjusted that one half looks downward into the water, and the other outward into the air. This character combined with the paddle-like hind legs would have served to distinguish the family. Again larvæ with a head and thorax modified to fit a circular burrow and with hooks on the dorsal surface of the fifth abdominal segment, which is supposed to be an adaptation to prevent the animals

from being drawn from their cylindrical burrows by
their prey, could serve to distinguish the entire family of
Cicindelidæ (tiger beetles). Such cases might be multi-
plied indefinitely.

Following Lamarck came Darwin, who, being more par-
ticularly a zoologist, was probably (proportionately, at
least) less familiar with structural response phenomena.
He was apparently impressed with the "fixity" of the
so-called adaptation characters in motile animals, and
with the fact that they are often family, generic or specific
characters. With the assumption that they originated in
the environment in which they are now found, Darwin
and his followers on the zoological side credited "natural
selection" of structural characters with the origin of
species. Though broader than Lamarck, this important
feature of Darwin's theory was quite clearly drawn from
data on motile animals. After the acceptance of Darwin's
theory, biologists were for many years engaged in elabo-
rating the ideas of phylogeny and natural selection by
working out recapitulations and homologies and by point-
ing out cases of adaptation. The investigation was
largely confined to the highly individuated animals. The
morphological method of this period, which indeed has
still continued in use among a minority of zoologists and
which finds a parallel in the recent morphological study
of the sex organs of plants, belongs to descriptive rather
than to analytical science. Since its conclusions are often
based upon the arrangement of species or of stages in
development into series chosen by the investigator, it is a
method which often allows free play of subjective fancy.
Thus unconsciously experimental study of modification by
environment became more and more neglected, and the
dominant type of investigation being such as to show
only the usual course of events in development, the ideas
of fixity grew more and more. Thus the fact that the
external form, structure and color of animals are not
easily modified without careful experimental methods,
and that the structural responses of sessile animals were

so little known, resulted in structure in animals being frequently regarded as fixed and every resemblance and peculiarity being too often regarded as significant. The explanations of supposed adaptations among animals fell largely to the theory of natural selection which was strained by some (see, for example, in Romanes, '92, p. 269) to explain origins in great detail, largely on the basis of the competition of species for food, etc. Explanations along this line were *carried to a reductio ad absurdum* as indicated by Livingston ('13) and have by no means disappeared from the scientific calendar. This tendency was less important on the plant side. More attention was given to speculation concerning adaptive response.

From a consideration of the facts just presented, we note that the characters of the two leading early view points in evolution were no doubt influenced if not actually caused to crystallize into their peculiar form by the failure of workers to recognize the entire series of phenomena which we have presented above. Thus a review of the responses of sessile and motile organisms throws much light on the influences leading to the first conceptions and later modification of these two leading doctrines. Botanists for many years dwelt mainly on the response of sessile organisms and crystallized a Lamarckian conception of the origin of adaptations through the fixing of advantageous responses as hereditary characters. During the same period zoologists essentially ignored sessile and other multiple individualed animals and their great plasticity and crystallized the Darwinian idea into Weismannian germplasm doctrine based on highly specialized single individualed animals.

3. Supposed Non-Inheritance of Response and the Germ Plasm Doctrine

The theory of the independence of the germ-plasm from the soma, and its continuity from generation to generation, was brought strongly to the attention of zoologists in 1885 by Weismann. It was the natural outgrowth of the methods and theories of the preceding period and

was largely based upon the non-inheritance of mutilations and the fact that the germ cells of a few organisms are, morphologically, early differentiated from the soma. Turning to its influence upon ideas concerning response, we note that from this viewpoint details of structure were not of fundamental importance unless traceable to the germ plasm. Still, structural details were more important than response, because, with the exception of instincts, responses were believed to occur *independently of the germ plasm* and hence were of interest only on their own account. Thus the methods used in applying Darwin's theory led to neglect of experimental study of response and culminated in the extreme views of Weismann. The germ-plasm theory or the ideas of heredity which are associated with it has dominated zoological thought almost if not quite down to the present day.[2]

4. The Influence of the Study of Response on Present-Day Biological Theory

One of the most striking developments of recent years has been the discovery that behavior responses are modifiable to a high degree. Small traces of reagents reverse

[2] Unconsciously suggestions of the supernatural which come up in connection with heredity and evolution have stimulated investigators to study and speculation, though they have often approached the question of heredity with an unscientific attitude. This is indicated by such statements as "I could not, however, resist the temptation to endeavor to penetrate the mystery of this most marvelous and complex chapter of life" and "the momentous issues involved" and "no more fundamental problem could well be stated" bear out this statement. The ardency which appears here and elsewhere in the discussion of scientific questions, appears to the writer to be associated with the discussion of problems which can not be referred to existing facts for solution. Few of the present generation of scientific men acquired a working knowledge of the methods of science before the age of twenty-five years, and the early habits of mind were formed in the atmosphere of the supernatural and dogmatic, which has characterized human thought for centuries. It is doubtful if the majority of us can maintain a scientific attitude for more than a short period; we must constantly come back to our tests and principles. This may account for many of the contradictions regarding scientific principles which one finds in the conversation of scientific men. When the methods of science have become the methods of society we may expect a group of scientific men far more effective than we ourselves can hope to be.

reactions. Intelligent behavior occurs in the lower Arthropods. Even *Paramœcium* shortens the time required to turn around in a tube, by repetition. Actions formerly regarded as instinctive now appear to be mere innate tendencies perfected by repetition. Thus the ideas of fixity have essentially disappeared from this field.

The response of organisms to injuries and the general control of form in the lower groups has done much to break down the ideas of fixity developed by Weismann and embryological schools. Thus Child, the leading American worker in this line, is able to control size, form, number of eyes in the case of Planarians. Various writers have found modifications inherited after several generations of repeated stimulation (see Bateson, '13). The development of anti-bodies (immunity) has been shown to be a response occurring in connection with many normal processes. The discovery of responses of so many types has led to abandoning ideas of fixity even among students of embryology and genetics. Thus we note the recent decline of the doctrine of continuity and independence of the germ plasm and kindred doctrines and points of view, which constitute the central ideas of fixity. It will accordingly be profitable to consider some further facts which make the germ-plasm doctrine unnecessary.

5. Aspects of the Untenability of the Germ Plasm Doctrine

The presence of primordial germ plasm is assumed even in sessile colonial organisms such as plants, cœlenterates, and in flatworms, etc., where under certain conditions any small part of the body may give rise to a complete organism. Here the theory is not needed to explain the facts.

Child ('11) said:

The theory of the continuity of the germ plasm as a system, independent of the soma, except as regards nutrition, has played an important part in biological thought during the last two decades, but I am convinced that it has led in the wrong direction and that it is re-

sponsible for many pseudo-problems of heredity and development, which on the basis of a different theory could never have occupied the attention and wasted the energy of biologists. Briefly my position is, that the gonad primordium is, at least up to a certain stage of development, physiologically a part of the individuality as are other organs, and that its further history of differentiation into male and female gametes indicates that it becomes specified in a particular direction, at least partly in consequence of its correlative environment in the organism.

The independence of the germ plasm is not well supported physiologically. Thus Wilson ('12, p. 163) says of the effect of prolonged ingestion of alkaline salts by mice:

> No obvious changes were evident in the liver, kidneys, lungs, spleen and intestines but in the testes some extraordinary alterations were found. These results are of especial interest because as the cells of the testes except the basal cells are regarded by many cytologists as out of coordination with the somatic cells. As a result of these experiments it would seem that they are more susceptible to changes in reactivity than the surrounding plasma.

Dungay ('13) and authors cited have thrown comparable light on this question.

The facts of embryology themselves are but a pseudo argument in its favor. The organisms in which continuity is supposedly demonstrable are highly individuated and their organs highly specialized and many different organs are early separated from the common mass of cells. The germ cells thus follow the general law of development in such animals. The germ plasm is probably no more independent of other parts of the organism than is the liver or any other special tissue. "Germ plasm" and "germinal continuity," if such exist, may thus be merely incidental to the particular type of organization of the specialized individuals in which they occur.

It should further be noted that on the botanical side this doctrine of the independence and continuity of the germ plasm has received little attention and has been given little credence because "germ plasm" arises from different tissues and is neither set aside early from the soma nor is it in any other sense clearly continuous.

Furthermore, the plasticity of plant structures made the application of the doctrine of natural selection to supposed adaptations untenable, and this type of explanation has received little more attention with botanists than have Lamarckian speculations with zoologists. The adaptation characters of plants can not ordinarily be used as taxonomic criteria (Coulter, '08).

6. The Measure of Values in Biological Science

One hears reference to pure science as something quite apart from applied science. It is indeed true that investigators in pure science are to some degree prompted to push forward in research by interest in the problems for their own sakes. But the human mind does not work long isolated from practical affairs or the main channels of human interest, and it is doubtful if the pure-science investigator continues long in this way. Observations are soon connected up in some way, actual or possible, with some human interest, be it as remote as the improving of human stock in remotely future generations. Thus *"pure science"* defined as investigation for investigation's sake hardly exists so far as the pure-science workers are concerned, but may be best defined as an *indirect* method of attacking problems of general importance. It differs from applied science in that application to practical problems is not its aim, though the estimated value of theories and results in ''pure'' science are often greatly modified by applicability to practical questions.

Certain problems and groups of facts in biology are sometimes referred to as *fundamental*. Some one has said that a fundamental problem is one the solution of which biologists have decided will give greatest progress. It is doubtless true that a few leaders reach such decisions with regard to particular questions, but the real causes of their general acceptance as fundamental are social and imitative. Thus when one investigator or a small group of investigators arrives at such a decision many others usually become active along the same lines largely because it is a popular topic. Thus under the influence

of a group of investigators among whom Weismann was a conspicuous leader, problems of the germ cells, the egg's early development, and heredity, became "fundamental problems." They evidently argued that since all comes from the egg and germ cell, all must be discoverable in the egg. If germ plasm were as independent from soma, as completely insulated from environment as continuous from generation to generation as has been assumed, the study of germ plasm would be the only way to the solution of the problems of heredity and evolution. This follows no matter whether the chromosomes or almost the entire egg are credited with carrying hereditary qualities; only the postulation of continuity and independence from soma and insulation from environment are necessary. If the independence of germ plasm from soma be accepted even in a weakened and modified form it follows that studies of somatic characters can at most be of secondary importance from the point of view of heredity and evolution. Thus in some quarters the value of various lines of zoological work has been estimated largely, unconsciously, no doubt, in proportion to the nearness or remoteness of their relation to the "*germ plasm*" question.

Thus it is true that in biology as in all other fields values are measured consciously or unconsciously by criteria. In recent years another better criterion of value has made its appearance among zoologists. The germ plasm criterion already discussed was primarily morphological; the second is physiological, borrowed no doubt from physiologists. It measures values on the basis of the analysis of the organisms into terms of physics and chemistry or is concerned with a mechanistic conception of life in all its manifestations. From this viewpoint the study of each and every part of the organism is important because the discovery of laws governing one part is usually or at least often of general importance. Investigations from this viewpoint have shown that the germ plasm criterion is clearly illogical in its application to the study of somatic characters because it is based upon the

tacit assumption that the soma is governed by *different laws* from the living matter which makes up the germ plasm from which it arose. In other words it is assumed that the germ plasm is so *different* from the soma that the discovery of laws governing the soma is a type of investigation of relatively little significance.

Some criterion of values is of course necessary in science as well as elsewhere, and for the sake of argument we would be willing to accept the second when broadly stated and the first when broadened and modified so as to accord with the second as appears to be the case among certain students of genetics. In other words, problems of the germ cells, the egg, and heredity, are of much importance when the germ cells themselves are regarded as dynamic and in their relations to the dynamics of the organism as a whole.

Granting that these are true and tenable criteria of values in present-day biological science, what is to be the method of application? Should biology demand that results be of direct application to these "central" problems? One has but to look at the history of almost any branch of science to find that great, if not the greatest, advances have come through following up results at points where relations to the central problems of the period were quite unsuspected, or by the transference of methods, principles and results from one field to another where relations between the two were not suspected. Take, for example, immunity and immunization, the history of which is ably sketched by Adami ('08, pp. 451–528). It has been known for ages that one attack of many infectious diseases yields more or less complete immunity from subsequent attacks. Thus for centuries in India and the East individuals, chiefly children, have been purposely inoculated with matter or by contact. The practise grew out of experience showing that diseases thus communicated to healthy individuals from weaker ones are less severe. In 1796 the results of Jenner on vaccination with cowpox were published. This may have influ-

enced Pasteur, who over eighty years later laid the
foundation for the modern epoch of development, by
combating a plague of diarrhœa in poultry (1880).
During the twenty years following, various investigators
added noteworthy contributions, and about 1900 Ehrlich
and Morgenroth evolved the ''side-chain theory'' by
which a large number of possible conditions can be pre-
dicted and all the observed facts of immunity explained.
While not expressed in strictly chemical terms, the theory
and the experiments which support it are very important
both practically and theoretically. In recent years the
knowledge of immunity and comparable phenomena have
been greatly extended. Various workers (Pfeffer, Vol.
II, p. 262) have shown similar phenomena in the increased
resistance of plants to poisons, thus making the responses
of plants and animals still more generally comparable.
Most recently workers on problems such as fertilization
(Lillie, '13), standing in close relation to the older germ-
plasm doctrine, have discovered facts belonging to this
field and made use of Ehrlich's theory to explain the ob-
servations. This development has helped to confirm the
conclusion of some investigators that immunity phe-
nomena represent important features of the chemical
mechanism of life. Adami has remarked,

> That a plague of diarrhœa in a poultry yard, studied by a professor
> of chemistry, should be the seed from which has grown the vast de-
> velopment of later years is a strange fact, but a fact nevertheless.

What was the attitude of pure science so called, of
germ-plasm doctrinairies, and biologists generally during
the long period which elapsed before they could make
use of his results? Clearly it was one of indifference, if
not disgust, toward the subject. The probable result of
such attitudes on the progress of the investigation of
immunity phenomena, had it not been for their immense
practical significance, is clear. They could not have
received their proper share of attention. Thus in the
pursuit of the analysis of the chemical mechanism of life
men who sought it directly have failed in this one impor-

tant step, and the chief contribution has come from very remote indirect methods. Generally speaking the investigators who choose a direct method of attack often put themselves somewhat in the position of the chemist who would make chemical analysis of *living* matter when his *first* step *defeats* its own purpose by killing the substance to be analyzed. The failure of exclusively direct methods is often evident. Still the ability to obtain results by the method of direct attack, combined with a far too rare ability to tie with them indirectly obtained data, sometimes gives noteworthy contributions.

It accordingly remains to be seriously considered whether or not biology can afford to apply criteria to the measure of the values of investigation. Their application is of course largely unconscious, but the effects are not thereby modified. Noteworthy results of their application are (*a*) concentration of work in certain lines indicated by a given criterion, and (*b*) an actual abandoning to a large degree of remote and indirect methods of attacking the problems which the criterion involves. This means the partial abandoning of the methods for which pure science stands.

Criteria can be safely used only in a very broad general way, and in application more often to past progress than to current investigation. They are perhaps most valuable as a guide to individual investigators working on problems remote from these more or less central ''pure science'' questions. That some guide should be in the hands of such workers is beyond question. In the hands of those attacking the problems directly they often appear detrimental because they soon take on an extreme form and become regarded as fundamental. At this stage they are usually in need of extensive revision. If the investigator is contributing observations and details only, he is doing a great service, for such information is needed everywhere. If he is able to combine his own and others results, he almost invariably draws data from all sources, *direct* and *indirect,* far and near. Granted the

ability to synthesize, the opportunity to use the ability sometimes comes to those who attack the so-called central problems directly. It comes equally often (we believe more often) to those who have led up to the central problem from some remote viewpoint, frequently condemned by the followers of direct method of attack. Granting the importance of synthesis, if the biologist seeks the solution of such a problem as the germ-plasm problem, he should encourage workers to start at points as *remote* from the subject as possible, that they may *approach it with new light and from new angles*.

In judging the work of another, its value should be determined more by the (*a*) strictness of scientific method used, (*b*) the thoroughness and completeness of the investigation, and (*c*) (and perhaps most important of all) evidence of ability to synthesize and combine other results with his own with a view to broader generalization. It must, however, also be recognized that there are many biological problems of much human importance, which must be solved quite independently of the ideal central problems of pure science.

6. Summary and Conclusions

From the data presented above, we note that the doctrine of purposeful, advantageous response (including anthropomorphic ideas) arose from the uncritical non-experimental study of the responses (structural) of sessile and (behavior) motile animals. The idea of the all-sufficiency of natural selection is largely the outcome of observational study of apparently fixed and yet apparently adaptive characters of *motile* highly individuated animals. The doctrine of the continuity of the germ plasm is likewise the outgrowth of the study of highly individuated animals in which the various organs are early differentiated in the dividing egg. No one of the doctrines is wholly tenable; no one is more than a partial truth. Each appears to have arisen from a recognition of certain more or less unconsciously selected and uncritically interpreted phenomena by each of several men

who secured different facts and attempted explanations.

In a few animals the ''germ plasm'' may be morphologically early differentiated and reasonably continuous, though governed by the same laws as other tissues. In others, any part of the general tissues may give rise to a complete organism. The behavior of some organisms is intelligent and purposeful, while that of others is largely mechanical. Some structural responses of sessile organisms are advantageous, some indifferent and some harmful. Some of the more fixed structures of the highly individuated animals are advantageous, some indifferent, and some disadvantageous (Metcalf, '13). No other type of general statement appears to be tenable, yet each extreme of each proposition has at some time or other been the subject of some all-inclusive doctrine.

Such are the limitations of an individual's knowledge and the psychic limitations of our race and generation. In considering the psychology of religion, Ames ('10, p. 394) points out similar well-recognizable tendencies in that field of human activity and quotes Cooley on social development as follows:

> Much energy has been wasted or nearly wasted, in the exclusive and intolerant advocacy of special schemes—single tax, prohibition, state socialism and the like, each of which was imagined by its adherents to be the key of millennial conditions. Every year makes converts to the truth that no isolated scheme can be a good scheme, and that real progress must be advanced all along the line.

Advance all along the line is what biological science must achieve. This I believe means the encouraging of all lines of indirect attack, whether they at first throw light on the ideal central question of pure science or important practical problems or not. It means the exercising of extreme caution in the application of criteria of values to scientific results. Such measures tend not only to stifle the best initiative in good investigators, but also tend to check the building up of fruitful hypotheses. The latter danger is greatest in connection with the mechanistic criterion referred to above. As has already been stated, criteria of values can be safely applied only

as broad general guides, and investigation should be measured on the basis of its thoroughness, the originality shown, etc.

In science special schemes of course do not exist recognized as such, but intolerant application of criteria· of values results in essentially the same condition.   One often hears the statement made by so-called scientific men, that this or that line of investigation has been pursued for several years, but has failed to yield important advances or generalizations, but they add, we will be very glad to recognize it as soon as its value is proven.   This seems to us to be a distinctly unscientific attitude, and but a polite modern statement of a spirit which in former generations often sent men to the stake or dungeon.   This is true because to these polite objectors its value is rarely or never proven.   It is "schemes" (preconceived theories) thus presented that have in the recent past stifled the study of responses by discouraging efforts in that direction and thus contributed materially toward making zoology the unorganized science which it is to-day.   We must recognize that the various aspects of zoology pure and applied have never been well correlated, less so we believe than in any other branch of natural science, clearly less than in botany.   In general, animal physiology has been isolated in medical schools and genetics, faunistics and morphology have not been properly influenced by it, while morphologists for many years held themselves aloof from other workers.

In a discussion dealing mainly with the doctrine of natural selection in the origination of adaptations, Mathews ('13) has sounded the keynote of a growing attitude toward all response questions.   Out of the infinite different combinations which may enter into the proteid molecule and the varying rates at which metabolic action may go forward, innumerable types of irritability and correlated structure have been and still are arising under the influence of environment external and internal. Of these some are incompatible with life, others indiffer-

ent, and others advantageous. Upon these physiological characters natural selection has operated to eliminate, and with time has perhaps rendered of less frequent occurrence, those characters that are incompatible with their conditions of existence. External form, color ornamentation, etc., while no doubt often of importance themselves are more often the advantageous or indifferent correlatives of physiological or irritability types which are compatible with their conditions of existence. The study of irritability and response may be pursued in many ways—by experiment, by observation in nature alone or combined with experiment. The mapping of stimulating conditions in nature, of the distribution of types of irritability and response, which is one function of field ecology and modern geography, can hardly fail to contribute materially to the advance of knowledge in many lines, including that of the physico-chemical mechanism of life. The student of experimental ecology has an infinite field of problems and methods thrown open to him by the organization of such information relative to responses. Still in our attempt to make advances along the line of the study of responses, we must not forget that it is but one of several lines of advance, all of which must sooner or later be correlated with a view to broader generalization.

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April 1, 1914

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AN APTEROUS DROSOPHILA AND ITS GENETIC BEHAVIOR

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AMONG the various mutants of the fruit-fly, *Drosophila ampelophila,* which have arisen from cultures in this laboratory, is one entirely destitute of wings, and hence called *apterous.*[1] The study of the heredity of this form has been difficult because of its almost complete (apparent) sterility. In order, therefore, to determine to which of the three groups of linked characters of *Drosophila* it belonged I was obliged, in most crosses, to make use of heterozygous flies that carried the factor for apterous. As this process is unique in certain regards, it will be described in some detail.

METHODS OF STUDY

At first it was thought that the apterous mutant was completely sterile, since none of the first flies, as they appeared occasionally in certain cultures, could be crossed even with normal individuals. At last, however, offspring were obtained from an apterous female by a wild male, and a permanent line started. But this line could not be perpetuated by means of apterous individuals, for these were unable to breed.[2] It had, therefore, to be kept up by means of heterozygous, winged flies. The method was as follows: The original cross of winged by apterous gave in F_2 approximately 3 winged to 1 apterous. Of the winged class approximately two thirds were heterozygous for apterous, and when mated together gave the same

[1] This apterous fly is quite distinct from that called wingless in earlier papers by Morgan, and now known as vestigial.

[2] Only twice, aside from the original mating, were apterous individuals successfully crossed, and then only to winged specimens, never to their own kind. These two cases are given in experiments II and III.

3 : 1 ratio. Selecting again from the winged flies, the proc-
ess could be repeated indefinitely. The only difficulty lay
in the fact that no visible character differentiated the
heterozygous from homozygous winged flies, and conse-
quently all matings had to be made in pairs taken at
random, with the result that about 56 per cent. of the
cultures were rendered worthless. In actual practise large
numbers were mated in pairs, and then all discarded save
those producing apterous.[3] This was the method used in
keeping up stock.

To obtain the necessary combination of apterous with
other mutant factors, winged offspring from apterous-
throwing parents were mated in pairs to flies of the
desired stock. One third of the normals from apterous
stock were pure for the normal allelomorph of apterous
and rendered worthless all matings in which they were in-
volved; but the other two thirds were heterozygous for
apterous, and when crossed with the desired stock gave
in F_2 some apterous offspring. If the F_1 flies were bred
en masse, approximately 15 winged to 1 apterous were ob-
tained, but if bred in pairs, certain pairs (those in which
both members were heterozygous for apterous) gave 3
winged to 1 apterous. The latter method was the one
actually used in most cases. In this manner the same end
result was attained as would have been secured by using
apterous individuals in crosses with other stocks, the
only difference being in the amount of labor involved in
making up a larger number of cultures. Both kinds of
crosses were, in fact, used, as will be seen below.

The use of symbols in this paper follows the system
recently adopted by Morgan and other students of *Droso-
phila* (Morgan, 1913, *a* and *b*). That is, for any pair of
allelomorphic characters a capital letter is used to indicate
the dominant, and a small letter the recessive factor—the
symbol being taken from the name of the mutant. Since
the apterous character is recessive, the symbols for the

[3] In the fourth experiment a character (black) was introduced which dif-
ferentiated homozygous from heterozygous and thus made it possible to pick
out the heterozygous individuals.

apterous fly become a_p–a_p, and those for the winged fly
A_p–A_p. In other words, A_p is a factor in the wild fly
necessary for wing production, while a_p is its modified
homologue responsible for lack of wings in the mutant.
The apparent contradiction in using A_p, not for the factor
responsible for apterous, but for its normal allelomorph,
may be confusing at first sight, but a little familiarity with
the system obviates this difficulty.

EXPERIMENTS

Experiment I.—Long-winged, red-eyed ♂ by apterous,
white-eyed ♀ (from miniature wing stock).

F_1 All winged.   Long-winged, red-eyed females.
                    Miniature winged, white-eyed males.

———

F_2 Winged and apterous as follows:

Winged {
Long-winged, red-eyed males and females.
Long-winged, white-eyed males and females.
Miniature-winged, red-eyed males and females.
Miniature-winged, white-eyed males and females.
}

Apterous {
Apterous, red-eyed males and females.
Apterous, white-eyed males and females.
}

This experiment shows the inheritance of the apterous
character to be Mendelian, giving in F_1 all winged, and in
F_2 approximately 3 winged to 1 apterous.   Table I con-
tains a summary of the offspring from 21 pairs of the F_1
and F_2 individuals, giving a total of 1,405 winged to 450
apterous,—a ratio of 3.12 to 1.

The absence of apterous flies in F_1 indicates at once
that the apterous character is not sex-linked.   The pres-
ence of miniature-winged flies in F_1 and F_2 indicates that
the apterous factor is independent of the miniature-wing
factor, which latter must have been carried by the apterous
female (coming from miniature wing stock), and trans-
mitted to her offspring unaffected by the apterous factor.

Analysis of the cross:

A_p, factor necessary for wing production. a_p, its allelomorph, in the apterous fly.

M, factor necessary for the production of long wings (sex-linked).

m, allelomorph of M responsible for miniature wings.

W, factor necessary for the production of eye color (sex-linked).

w, allelomorph of W responsible for white eyes.

P_1 Long, red male $A_pMWX–A_p$,
       Apterous, white female $a_pmwX–a_pmwX$.
F_1 Long red females $A_pMWX–a_pmwX$,
       Miniature white males $A_p–a_pmwX$.

F_2, leaving out of account the sex-linked factors and considering only winged vs. apterous:

Gametes of F_1 A_p, a_p.
                   A_p, a_p.

F_2 $\begin{cases} A_p–a_p. \\ A_p–A_p. \\ A_p–a_p. \end{cases}$
    Winged

Apterous $a_p–a_p$.

Experiment II.—Long vermilion ♀ by apterous, white ♂.[4]

This cross is practically the reciprocal of Exp. I, except that vermilion replaces red eye color in the winged parent. Like Experiment I it involves two pairs of sex-linked characters, aside from the apterous character. The results are essentially like those of Experiment I and may be passed over briefly.

P_1 Long, vermilion ♀ $A_pMWX–A_pMWX$,
        Apterous, white ♂ $a_pmwX–a_p$.[4]

[4] The white-eyed, apterous ♂ in this cross is white-vermilion, *i. e.*, the double recessive, and therefore when crossed with vermilion it gives vermilion instead of red in F_1.

F$_1$ Long, vermilion ♀ $A_pMWX–a_pmwX$,
      Long, vermilion ♂ $A_pMWX–a_p$.

F$_2$ Long vermilion ♀ and ♂
      Long, white ♂   ⎫
      Miniature, vermilion ♂   ⎬ Winged.
      Miniature, white ♂   ⎭

      Apterous, vermilion ♀ and ♂ ⎫
      Apterous, white ♂   ⎬ Apterous.

TABLE I

OFFSPRING FROM PAIRS HETEROZYGOUS FOR APTEROUS IN EXPERIMENT I.
PARENTS TAKEN FROM F$_1$, F$_2$ AND F$_3$

Mating No.	Winged	Apterous	Ratio
41	122	32	3.8 : 1
53	41	14	2.9 : 1
56	29	12	2.5 : 1
64	46	30	1.5 : 1
65	29	16	1.8 : 1
80	85	28	3.04: 1
83	71	20	3.5 : 1
84	13	3	4.3 : 1
85	40	9	4.4 : 1
111	183	64	2.8 : 1
112	20	10	2 : 1
117	99	42	2.4 : 1
118	28	10	2.8 : 1
130	32	7	4.5 : 1
131	76	26	3.1 : 1
132	71	19	3.7 : 1
134	92	36	2.6 : 1
151	58	12	4.8 : 1
170	78	10	7.8 : 1
171	63	15	4.5 : 1
177	129	35	3.6 : 1
	1,405	450	

Average ratio of winged to apterous, 3.12:1.

An analysis of the F$_2$ is not essential here and is omitted for the sake of brevity. It may be derived from the F$_1$ formulæ. Table II indicates the expected classes and ratios in F$_2$ and gives the actual numbers obtained in culture No. 59, in which each class was recorded separately. In subsequent cultures of this experiment no attempt was made to separate any but the winged and apterous classes. Counts of the latter are given in Table III.

TABLE II

MATING 59

F₂ — Expected Classes	Expected Ratio	Actual Ratio	Actual No.
Long verm. ♀	12	13.8 : 1	185
Long verm. ♂	3	4.2 : 1	57
Long white ♂	3	2.4 : 1	31
Miniature verm. ♂	3	2 : 1	26
Miniature white ♂	3	4 : 1	53
Apterous verm. ♀	4	3.2 : 1	44
Apterous verm. ♂	2	1.2 : 1	15
Apterous white ♂	2	2 : 1	24

TABLE III

F₂ FROM MASS CULTURES

Culture No.	Winged	Apterous	Ratio
58	367	78	4.7 : 1
59	352	83	4.2 : 1
96	556	114	4.8 : 1
97	306	70	4.3 : 1
120	597	103	5.08: 1
135	554	104	5.3 : 1
137	405	49	8 : 1
154	298	45	6.6 : 1
157	405	53	7.6 : 1
	3,840	699	Average ratio, 5.5 : 1.

F₂ FROM PAIRS

Culture No.	Winged	Apterous	Ratio
155	141	35	4.1 : 1
156	38	11	3.4 : 1
	179	46	Average ratio, 3.9 : 1.

F₃ FROM PAIRS

Culture No.	Winged	Apterous	Ratio
160	119	25	4.7 : 1
162	123	27	4.6 : 1
172	266	62	4.3 : 1
173	87	26	3.4 : 1
174	165	37	4.5 : 1
175	167	42	4 : 1
176	171	46	3.7 : 1
177	129	35	3.6 : 1
178	92	23	4 : 1
	1,319	323	Average ratio, 4.08: 1
	179	46	
	1,319	323	
Total from pairs,	1,498	369	Ratio, 4.6 : 1.

It will be noted that the apterous classes fall a little below the expected numbers in most cases. This is characteristic of all weak races of *Drosophila*, and is doubtless due to the inability of some flies to mature. Of the winged classes the first two and the fifth exceed the Mendelian ratios, while the other two fall short, due to linkage between white, vermilion and miniature.[5] The distribution of apterous, however, is entirely independent of the others, showing that the factor responsible for it is not a member of the group containing those responsible for vermilion eyes, white eyes, or miniature wings.

The ratio of winged to apterous in this particular culture is 4.2:1. Table III includes a summary of this and nineteen similar cultures in which the parents were all descendants of the long-winged, vermilion-eyed female by the apterous male mentioned above. The first nine are mass cultures, the next two are pairs, from F_1 flies. Below these are offspring from nine pairs of F_2 flies.

It is noticeable that the ratio of apterous to winged is greater in cultures where pairs are used than in mass cultures, though all parents in the latter are heterozygous. This, I believe, is unquestionably due to the low viability of the apterous flies, which prevents some of them from maturing in cultures where the competition is severe. For this reason the averages are given separately for pairs and for mass cultures. The average from pairs is 4.06:1, while that from mass cultures is 5.5:1. This low viability is also shown by pairs, if the food conditions are not good, or if the culture becomes very dry.

Experiment III.—To determine the relation between apterous and characters in Group III.

It is obvious from Experiments I and II that apterous is not a sex-linked character (Group I). The present experiment is for the purpose of determining its relation to characters of Group III. As a representative of the latter group pink eye color was chosen. The results of the cross between this and apterous may be passed over briefly

[5] For d scussion of linkage between these characters see Morgan, 1911.

since they are similar to previous results in showing no
linkage. A winged, pink-eyed male bred to an apterous,
vermilion-eyed female (from Experiment III) gave, as
expected, winged, vermilion-eyed males and winged, red-
eyed females in F_1. These inbred gave four classes of
winged and four classes of apterous, *i. e.*, red, vermilion,
pink and orange.[6] The ratios are such as to show inde-
pendent segregation of apterous and pink. Below is a
summary of the expected and actual results.

$$P_1 \quad \text{Apterous, vermilion } \female \quad a_p v P X - a_p v P X,$$
$$\qquad \text{Winged, pink } \male \qquad\quad A_p V p X - A_p p.$$

$$F_1 \quad \text{All winged.} \quad \text{Red } \female \quad a_p v P X - A_p V_p X,$$
$$\qquad\qquad\qquad\quad \text{Verm. } \male \quad a_p v P X - A_p p.$$

Eight kinds of eggs and four kinds of spermatozoa are
formed by these F_1 flies, giving, through random fertiliza-
tion, 32 classes of offspring divided into eight groups, as
shown in Table IV.

TABLE IV

F₂ Expected Results			Actual Results in Experiments					
Classes	Ratio		627	628[7]	629	630	631	Total
Winged, red............	9 } 9		85 } 143	34	120	35	70	402
Winged, vermilion.......	9		58					
Winged, pink...........	3 } 3		25 } 35	3	38	11	24	111
Winged, orange.........	3		10					
Apterous, red...........	3 } 3		22 } 35	15	32	11	21	114
Apterous, vermilion......	3		13					
Apterous, pink..........	1 } 1		7 } 15	0	10	2	7	34
Apterous, orange........	1		8					

In the table red and vermilion have been considered
together as one class, because they both contain P; and
similarly pink and orange have been considered together
because they both contain p. The total numbers for the
four classes give the ratios $402 : 111 : 114 : 34$, or $10.8 : 3.6 :
3.35 : 1$,—a sufficiently close approximation to the expected

[6] Orange eye is the double recessive $pv-pv$.

[7] In this culture the ratios are seen to diverge widely from the expected,
due, I believe, to the poor cultural conditions in this case which prevented
some of the weaker pink and orange flies from maturing

9:3:3:1. These results clearly show the independence (*i. e.,* lack of linkage) of apterous and pink.

Table V includes all matings (giving apterous) in Experiment III, for the purpose of showing the ratio of winged to apterous.

TABLE V

Mating No.	Winged	Apterous	Ratio
627	178	50	3.56 : 1
628	37	15	2.47 : 1
629	158	42	3.7 : 1
630	46	13	3.53 : 1
631	94	28	3.36 : 1
646	48	10	4.8 : 1
649	81	27	3.1 : 1
650	44	14	3.15 : 1
651	124	37	3.35 : 1
652	92	34	2.7 : 1
674	50	19	2.63 : 1
692	75	27	3.15 . 1
	1,027	316	

Average ratio winged to apterous, 3.25:1.

Experiment IV.—To determine the relation between apterous and characters in Group II.

The mutant called "black" (having black body and wings) was used in this experiment as a representative of Group II. No direct matings with apterous individuals, such as obtained in the three preceding cases, could be effected here, and consequently the winged brothers and sisters of apterous had to be used for crossing with black, according to the method described in the introduction. Matings of this kind (in pairs) gave, in F_1, winged flies, some of which were heterozygous for apterous and black. These inbred (also in pairs) gave winged and apterous, and gray and black, as shown below:

P_1 Black ♂ homozygous for wings $A_p b - A_p b$,
      Gray ♀ heterozygous for apterous $A_p B - a_p B$.

F_1 Winged, heterozygous for black · $A_p b - A_p B$,
      Winged, heterozygous for black and apterous $A_p b - a_p B$.

Only pairs in which both members were of the second type ($A_p b - a_p B$,—heterozygous for apterous) could pro-

duce apterous. The others, therefore, are ignored. Considering the second type alone, the analysis becomes:

F_1 gametes (expected) $A_pb–A_pB–a_pb–a_pB,$
$A_pb–A_pB–a_pb–a_pB.$

F_2 Expected classes.

$a_pB–a_pB$	apterous, gray.
$a_pB–a_pb$	apterous (heterozygous for black).
$a_pB–A_pB$	winged, gray.
$a_pB–A_pb$	winged, heterozygous for black.
$a_pb–a_pB$	apterous, heterozygous for black.
$a_pb–a_pb$	apterous, black.
$a_pb–A_pB$	winged, heterozygous for black.
$a_pb–A_pb$	winged, black.
$A_pB–a_pB$	winged, gray.
$A_pB–a_pb$	winged, heterozygous for black.
$A_pB–A_pB$	winged, gray.
$A_pB–A_pb$	winged, heterozygous for black.
$A_pb–a_pB$	do.
$A_pb–a_pb$	winged, black.
$A_pb–A_pB$	winged, heterozygous for black.
$A_pb–A_pb$	winged, black.

Expected ratios: 3 winged black; 6 winged heterozygous for black; 3 winged gray; 1 apterous black; 2 apterous heterozygous for black; 1 apterous gray.

Actual results: winged black, winged heterozygous for black, and apterous gray, as shown in Table VI.

In the last two matings black and heterozygous offspring were counted as one class.

Total: winged 701; apterous 174 or 4.02:1.

The expectation for the F_2 if A_p and B segregate independently is equal numbers of black and gray among the winged and among the apterous offspring. Actually, however, the apterous flies are all gray, and the winged flies are all black or heterozygous for black. Furthermore, the

ratio of heterozygotes to pure blacks in the winged class shows that the flies which should have been gray according to expectation have been added to the heterozygotes. Likewise the gray flies in the apterous class are about four times as numerous as anticipated, showing that the expected heterozygotes and blacks are here gray. From this it is evident that the factors a_p and B, on the one hand, and A_p and b, on the other, have remained associated in the combination which they formed in the parents, instead of independently segregating. Such an explanation accounts for the absence of A_pB and a_pb gametes in the F_1 generation, and consequently for the absence of gray, winged flies, and of black or heterozygous apterous flies in F_2. The evidence accords with that obtained for many other mutant characters in *Drosophila*, and the explanation is the same as that given for the previous cases (*e. g.*, Morgan, 1911, 1912; Morgan and Lynch; Sturtevant, 1913 *a* and *b;* Dexter).

TABLE VI

ACTUAL RESULTS

Mating No.	Winged			Apterous		
	Gray	Black	Heterozygous	Gray	Black	Heterozygous
703	0	15	52	18	0	0
724	0	22	71	26	0	0
732	0	20	54	15	0	0
733	0	29	59	15	0	0
741	0	19	50	19	0	0
745	0	35	86	30	0	0
746	0	15	42	13	0	0
		155	414	136		
725		53		14		
734		79		24		

The presence of a definite linkage or association between apterous and black (*i. e.*, between either a_p or A_p and b or B depending upon the nature of the cross) as shown by this experiment, together with the absence of any such linkage with characters in Groups I and III, as shown by the preceding experiments, indicate that apter-

ous is a member of Group II and is, presumably, associated or linked with all other characters belonging to that group.

Supposedly this association of the characters results from an association of the factors responsible for them in the germ cells. And this latter association has been explained upon the assumption that factors responsible for linked characters are located in the same chromosome. The hypothesis has even been carried so far as to postulate a linear arrangement of the factors within the chromosome—the relative position of the factors being determined by the degree or amount of linkage existing between them. This conception and the data upon which it is based have been amplified by Morgan and by Sturtevant, and need not be dwelt on here. In the present case no attempt has been made to ascertain the exact degree of linkage between apterous and other characters in the group, except black, because of the difficulty of breeding the apterous flies. Apparently the linkage between apterous and black is very close, if not complete, since no case of "crossing over" was observed among the 875 F_2 offspring in this experiment (Table VI). There is a possibility that the classification of the F_2 apterous flies as all gray is not absolutely correct, because, owing to the difficulty of distinguishing gray from heterozygous black in apterous specimens, an occasional heterozygous fly might have passed for pure gray. However, if there had been any appreciable number of cross-overs in this direction, there would also have been some in the opposite direction, which fact would have been indicated by the presence of winged, gray flies. And since none of these were observed, it is safe to conclude that few or no cross-overs occurred, and hence that apterous is very closely, if not completely, linked to black.

Experiment V.—To determine the relation between the apterous mutant and the "vestigial" mutant.

Among the mutant characters of Group II is one called "vestigial wing." Flies having this character are more

like the apterous individuals than are any of the other mutants, and since the two characters belong to the same group the question arose as to whether or not the factor responsible for one might be simply a modification of that responsible for the other. Experiment V was performed to determine this point.

Long-winged flies heterozygous for apterous were crossed with vestigial winged individuals, and F_1 and F_2 generations raised. The F_1 flies were all long winged, which fact in itself indicates the independence of the two characters, for if they were allelomorphs either apterous or vestigial should have appeared. In F_2 both vestigial and apterous, as well as long-winged, flies appeared, showing conclusively the independence of the two characters.

Summary of Experiments

Experiments I and II show that the apterous character is a simple Mendelian recessive, which independently mendelizes with miniature wings, white eyes and vermilion eyes, and hence is not sex-linked (*i. e.*, not a member of Group I).

Experiment III shows that the apterous factor is transmitted independently of the factor for pink eye, thus indicating that apterous is not a member of Group III.

Experiment IV shows a linkage ratio to result from crosses involving apterous and black, the ratio being such as to indicate a very close linkage between apterous and black, and to identify apterous as a member of Group II.

Experiment V shows apterous to be distinct from vestigial wing, to which it bears a considerable degree of resemblance.

Origin and Characteristics of the Apterous Mutant

The description of the apterous fly has been deferred up to this point in order that it might be combined with a discussion of the experimental results.

The mutant has appeared upon several occasions, but

always in the same stock (miniature white), and always with the same evidence of weakness and low viability. Fig. 1 is a camera drawing of a typical specimen, made by Miss E. M. Wallace. In morphological characters the fly differs from the normal in being entirely destitute of wings and in possessing greatly reduced balancers. Likewise in physiological characters it deviates strikingly from the normal.

FIG. 1.   APTEROUS MUTANT OF Drosophila ampelophila.

This is best shown by means of a comparison between apterous flies and normal flies from which the wings have been removed. The latter are not appreciably inconvenienced by their loss of wings; they show characteristic vigor in their active running and jumping movements, they easily right themselves if overturned, or extricate themselves if entangled in food or cotton, and they are long lived and breed as prolifically as do winged individuals. In fact they show no ill effects except the inability to fly. The true apterous individuals, on the other hand, show marked abnormalities in all these respects. Instead of being vigorous and active they are weak and usually sluggish; if overturned they have great difficulty in righting themselves; or, if entangled in food or cotton, they are usually unable to extricate themselves and consequently perish. Moreover, they are always short lived, even when kept under the best possible conditions and prevented from becoming entangled in food or cotton. And lastly they exhibit a most marked inability to breed, as noted in the experiments. This characteristic, as has been mentioned above, is so marked that the apterous flies were at first thought to be sterile. I am convinced now, however, that the difficulty is not one of sterility at all, but is due to a physical weakness which makes it extremely difficult for the flies to copulate, and for the females, even when fertilized, to produce and lay eggs. Cytological examination has shown that the males produce spermatozoa in an apparently normal manner, yet prolonged observation of

the flies has not revealed a single copulation or attempt at copulation on the part of an apterous male.[8] Similarly the females have been shown to produce rudimentary eggs in an apparently normal manner, and in two cases females have produced offspring when fertilized by winged males, thus indicating their fertility. But many other cases have been observed in which apterous females were fertilized by winged males (or at least in which copulation took place), and yet in these observed cases the females invariably died without producing offspring,[9] because, I believe, of their physical weakness.

From these facts it appears practically certain that the apparent sterility is not due to infertility of either sperm or eggs, but results from a weakness which makes it very difficult for the apterous flies to perform the reproductive processes.

This explains why no crosses have been secured between apterous and apterous, although each sex has been successfully crossed to winged. It is also supported by the fact that from the cross between apterous male and winged female a large number of offspring were secured, since the winged female could produce many eggs,—whereas in the two crosses between apterous females and winged males only a very few offspring were secured, because the apterous females could only produce a few eggs.

When the experiments were first begun it was hoped that sooner or later one or more inherently vigorous apterous flies would appear which might give rise to a vigorous race. But nothing of the sort took place, although numbers of the apterous flies were given opportunity to breed all through the course of the experiments. Obviously, then, the physiological characteristics, as

[8] Copulation in normal flies can be observed with very little difficulty. It is evident that at least one case of copulation by an apterous male occurred, namely in Experiment II.

[9] Judging from the cases observed a large number (probably one hundred or more) of apterous females must have been fertilized by winged males during the course of these experiments, yet only three of these gave progeny.

shown by vigor and viability, are directly associated with morphological characters and are not to be separated from them by selection. In other words, the "factor" responsible for lack of wings is also responsible for physiological disturbances.

The only suggestion of an inherent difference between different races, or strains of apterous, is the slight difference in the percentage of apterous offspring in Experiments I and III as compared with II and IV. In I and III the ratios of winged to apterous are 3.12 : 1 and 3.24 : 1, respectively, while in Experiments II and IV they are 4.06 : 1 and 4.02 : 1. This deviation is not great, but it is fairly constant, and is sufficient, I believe, to indicate a real difference. But whether it is to be explained upon the assumption that in I and III the apterous parents were inherently stronger than in II and IV is not so clear. It might equally well be explained upon the basis of differences in the winged races to which apterous was crossed. Unfortunately, an experimental analysis of the question is prohibited by the difficulty of breeding the apterous flies, and it must, therefore, be left open. One fact, however, is clear, namely that there is no progressive increase in viability of the apterous flies, for the apterous parent in Experiment II, where the viability appears to be low, was descended directly from that in I where it appears to be high, and likewise the parent from the apterous side in IV was obtained directly from III.

In conclusion it may be profitable to call to mind briefly the bearing of certain of the above data on the question of the nature and behavior of Mendelian "factors."

The present case of a definite correlation between lack of wings, reduction in size of balancers, and weak physical constitution in the apterous race of *Drosophila,* shows clearly that one factor may have far reaching effects, and not be limited to any particular part or organ,—a fact

which has been long known, and often mentioned,[10] but by no means universally recognized.

Correlated with, or resulting from this principle is the conception that the final result of ontogenetic development is not due to the *independent* action of various factors and their products, but is due to the *combined* action, or the *interaction* of these products during development. To illustrate by the wing of a fly,—it is probable that the normal development of such an organ is not dependent solely upon one factor, but that it is influenced by many factors. This is strongly suggested by data derived from the various wing mutations in *Drosophila*. These have dealt with a large number of factors, each of which is responsible for a definite wing modification. For instance, one factor is responsible for miniature wings, another for vestigial, another for rudimentary, another for curved, etc.[11] From the fact that these mutant factors (which may be considered as modifications of factors in the normal fly) influence the wings, it seems highly probable that their normal allelomorphs also influence wing production in the wild fly.

Finally I wish to thank Dr. T. H. Morgan for kindly assistance and advice in connection with this work.

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[10] Most recently, perhaps, by Morgan (1913a, page 9): ''A change in a factor may have far-reaching consequences. Every part of the organism capable of reacting to the new change is affected. Though we seize upon the most conspicuous difference between the old type and its mutant, and make use of this alone, every student of heredity is familiar with cases where more than the part taken as the index is affected. Weismann's theory, on the other hand, seems to identify each character with a special determinant . . .''

[11] The same is true for various eye colors, and body colors.

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SHORTER ARTICLES AND DISCUSSION

FORMULÆ FOR THE RESULTS OF INBREEDING

In connection with Pearl's recent valuable analyses of the
results of inbreeding (1, 2, 3), a comparison of these results with
those from self-fertilization is of interest.   In my note on the
latter (4), I gave a formula for the rate at which organisms
become homozygotic through continued self-fertilization.   This
occurs more slowly in the various types of inbreeding, but Pearl
gives no general formula for it.   For purposes of comparison I
have worked out from Pearl's data the general formula for the
rate at which organisms become homozygotic through continued
brother by sister mating; as such formulæ appear to be of perma-
nent value, it is here given.[1]   What the formula gives is, pre-
cisely, (1) the proportion of individuals that will be homozygotic
for any given character after any number of unbroken genera-
tions of such inbreeding, (2) the average proportion of the char-
acters of a given individual that will be homozygotic after any
number of unbroken generations of such inbreeding.   The nu-
merical value so obtained may conveniently be called the co-
efficient of homozygosis.

The formula turns out to be a combination of the successive
powers of 2, with the successive terms of the Fibonacci series,
which appears in so curious a way in various natural phenomena.
In this series every term is the sum of the two preceding terms,
the series beginning: 0, 1, 1, 2, 3, 5, 8, 13, etc.

Let $x =$ the coefficient of homozygosis.

$n =$ the number of inbred generations (the number of
    times successive brother by sister mating has
    occurred).

f_1, f_2, f_3, etc., $=$ the successive terms of the Fibonacci series
    (thus $f_1 = 0$, $f_2 = 1$, etc.).

Then the formula for the coefficient of homozygosis is:

$$x = \frac{2^{n-1} + f_1 \cdot 2^{n-2} + f_2 \cdot 2^{n-3} \ldots \text{ etc.}}{2^n}$$

(The terms in the numerator are continued until the exponent
of 2 becomes 0.)

[1] In conversation, Dr. Pearl urged the publication of the present note,
otherwise I should not at this time have dealt with a matter which he has
under analysis.

Thus, if the number of inbreedings (n) is 1.

$$x = \frac{2^0}{2^1} = 1/2, \text{ or } 50 \text{ per cent.}$$

If $n = 4$

$$x = \frac{2^3 + 0 \cdot 2^2 + 1 \cdot 2^1 + 1 \cdot 2^0}{2^4} = 11/16, \text{ or } 68.75 \text{ per cent.}$$

If $n = 9$

$$x = \frac{2^8 + 0 \cdot 2^7 + 1 \cdot 2^6 + 1 \cdot 2^5 + 2 \cdot 2^4 + 3 \cdot 2^3 + 5 \cdot 2^2 + 8 \cdot 2^1 + 13 \cdot 2^0}{2^9}$$

$$= 457/512, \text{ or } 89.26 \text{ per cent.}$$

If $n = 16$

$$x = \frac{63819}{65536} \text{ or } 97.38 \text{ per cent.}$$

As these examples show, the formula gives the results that were obtained by Pearl in the detailed working out (so far as this was carried), as given in Pearl's table I (2, p. 62). (It will be noted that Pearl counts as generation *1* the one *before* inbreeding has occurred, so that his generation 10, for example, is that in which there have been 9 inbreedings $(n=9)$.)

If one is working out the values of the coefficient x for a series of generations, the above formula may be expressed as a simple rule, applicable after the value for $n=1$ is obtained. This rule is:

The value of the coefficient of homozygosis x for any term (as the nth) is obtained by doubling the numerator and denominator of the fraction expressing the value for the previous term, and adding to the numerator the corresponding (n — 1th) term of the Fibonacci series.

Or, in view of the peculiar nature of the Fibonacci series, the rule may be expressed as follows:

Double the numerator and denominator. and add to the numerator the sum of the last two numbers so added.

Thus, since

$$x \text{ for 1 inbreeding} = 1/2$$

$$x \text{ '' 2 '' } = \frac{2 \times 1 + 0}{2 \times 2} = 2/4$$

$$x \text{ '' 3 '' } = \frac{2 \times 2 + 1}{2 \times 4} = 5/8$$

$$x \text{ '' 4 '' } = \frac{2 \times 5 + 1}{2 \times 8} = 11/16, \text{ etc.}$$

After obtaining x, or the proportion of homozygotes for any one pair of characters, the proportion y for any number m of pairs is obtained simply by raising x to the mth power, that is:

$$y = x^m.$$

Thus, after two generations of brother $\times$ sister mating, the proportion of homozygotes for three pairs of characters is $(1/2)^3 = 1/8$, or 12.5 per cent. After 8 generations of such inbreeding the proportion homozygotic for 10 pairs of characters is:

$$\left(\frac{222}{256}\right)^{10} = 24.05 \text{ per cent.}$$

The corresponding value in the case of continued self-fertilization is 99.61 per cent. (4, p. 491).

Whether it may be possible to obtain a similar formula for the coefficient of homozygosis in the cases of mating of cousin $\times$ cousin or of parent $\times$ offspring, remains to be discovered.

Pearl's "coefficient of inbreeding" gives the percentage of *lacking* ancestors in a given pedigree, as compared with the number that would be present if all the parents were unrelated. In order to compare self-fertilization with inbreeding in this respect, Pearl's formulæ for the coefficient of inbreeding may be expressed in terms of the number of successive inbreedings (n); for many purposes the formulæ appear more convenient so expressed. The following gives these formulæ for self-fertilization and the three types of inbreeding, together with those, so far as worked out, for the proportion of individuals homozygotic with respect to a given character. In all these, n is the number of successive self-fertilizations or inbreedings.

	Coefficient of Inbreeding.	Coefficient of Homozygosis.
Self-fertilization	$\dfrac{2^n - 1}{2^n}$	$\dfrac{2^n - 1}{2^n}$
Brother $\times$ Sister	$\dfrac{2^n - 2}{2^n}$	$\dfrac{2^{n-1} + f_1 \cdot 2^{n-2} + f_2 \cdot 2^{n-3} \cdots \text{etc.}}{2^n}$
Cousin $\times$ Cousin	$\dfrac{2^{n-1} - 2}{2^n}$	?
Parent $\times$ Offspring	$\dfrac{2^n - n - 1}{2^n}$	?

It will be observed that in self-fertilization the value of the coefficient of inbreeding is, curiously, the same as that of the coefficient of homozygosis, while in the other cases there is no evident simple relation between the two. Further, the coefficient

of inbreeding in brother × sister mating is the same as for self-fertilization, save that it lags one generation behind the latter; thus the coefficient for the fourth generation of self-fertilization is the same as that for the fifth of brother × sister mating. Pearl (1, p. 592) has already pointed out that in cousin mating the coefficient is one-half that for brother × sister, with a lag of one generation; as compared with self-fertilization the lag is two generations. No such simple relation is apparent between the proportions of homozygotes resulting from the diverse methods of breeding, though possibly such may yet be discovered.

<div align="right">H. S. Jennings</div>

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A SHORT-CUT IN THE COMPUTATION OF CERTAIN PROBABLE ERRORS

In his handbook of statistical methods, on p. 38, Dr. C. B. Davenport[1] gives a short method for the calculation of the probable errors of some of the commonest statistical constants, in a table of logarithmic formulæ. It would seem that the simple and obvious short-cut involved has not been given the attention it deserves in connection with non-logarithmic calculation. The logarithmic formulæ are as follows:[2]

$$(1)\ \log E_A = \log .6745 + \log \sigma - \tfrac{1}{2} \log n \left[\text{since } E_A = .6745\, \frac{\sigma}{\sqrt{n}} \right],$$

$$(2)\ \log E_\sigma = \log E_A - \tfrac{1}{2} \log 2 \left[\text{since } E_\sigma = .6745\, \frac{\sigma}{\sqrt{2n}}, \quad \text{or,}\quad E_\sigma = E_A \div \sqrt{2} \right],$$

[1] Davenport, C. B., ''Statistical Methods with Special Reference to Biological Variation,'' 2d ed., 1904, New York, John Wiley & Sons.

[2] A indicates the weighted arithmetic mean, σ the standard deviation, and C the coefficient of variability.

$$(3)^3 \qquad \log E_C = \log E_\sigma - \log A \ [\text{since } E_C = E_\sigma \div A].$$

Now, if one is working with a calculating machine, he can simply carry the value of E_A to two or three more decimal places than are to be retained, and then divide by the square root of 2 to get E_σ; similarly, the latter value, divided by the mean, gives E_C.

The writer prefers, however, to calculate the values in the ordinary way on the machine, using Miss Gibson's[4] table for $\dfrac{.6745}{\sqrt{n}}$ and $\dfrac{.6745}{\sqrt{2n}}$, and then to use the short method in checking. The original computations can be indicated and performed with great confidence and rapidity, since it is hardly possible to make an error that will not be discovered in the checking.[5] It is obviously safer, as well as much quicker, to check in this way than to repeat the original processes. HOWARD B. FROST

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GALTON AND DISCONTINUITY IN VARIATION

IT seems not to be generally realized that Galton recognized both continuity and discontinuity, both in variation and inheritance. Of course, all biologists are familiar with "Galton's polygon," in which slight oscillations of the polygon on one of its faces, but without a change of face, are compared with "small unstable deviations" (fluctuations), while a larger oscillation, in which the polygon moves over to a new face, is compared to a sport . . . of such marked peculiarity and stability as to rank as a new type, capable of becoming the origin of a new race with very little assistance on the part of natural selection.[1]

Galton's polygon illustrated for him how the following conditions may co-exist:

(1) Variability within narrow limits without prejudice to the purity of the breed. (2) Partly stable sub-types. (3) Tendency, when much disturbed, to revert from a sub-type to an earlier form. (4) Occasional sports which may give rise to new types.

These four types would seem to correspond rather well to what

[3] Formula (3) gives, of course, the approximate or uncorrected value of E^C.

[4] Gibson, Winifred, "Tables for Facilitating the Computation of Probable Errors," *Biometrika*, 4: 385–393. 3 tables.

[5] Unless, of course, one misreads the figures from the machine in checking.

[1] "Natural Inheritance," London, 1889, p. 28.

are now called (1) fluctuations or ''non-inherited'' (in reality, I think, partially inherited) continuous variations; (2) instability resulting from a heterozygous or partially heterozygous condition; (3) reversions, now believed to result chiefly from crossing; and (4) mutations.

Galton is equally explicit in other statements on this subject. Like Darwin, he admitted the facts both of continuity and discontinuity in variation; but, unlike Darwin, he also recognized discontinuity or alternation as well as continuity or blending, in inheritance. Thus he says, in a paragraph headed ''stability of sports'':[2]

Experience does not show that those wide varieties which are called '' sports '' are unstable. On the contrary, they are often transmitted to successive generations with curious persistence. Neither is there any reason for expecting otherwise. While we can well understand that a strained modification of a type would not be so stable as one that approximates more nearly to the typical center, the variety may be so wide that it falls into different conditions of stability, and ceases to be a strained modification of the original type.

In another paragraph,[3] headed ''Evolution not by minute steps only,'' he says:

The theory of evolution might dispense with a restriction, for which it is difficult to see either the need or the justification, namely, that the course of evolution always proceeds by steps that are severally minute, and that become effective only through accumulation. That the steps *may* be small and that they *must* be small are very different views; it is only to the latter that I object. . . . An apparent ground for the common belief is founded on the fact that wherever search is made for intermediate forms between widely divergent varieties, whether they be of plants or of animals, of weapons or utensils, of customs, religion or language, or of any other product of evolution, a long and orderly series can usually be made out, each member of which differs in an almost imperceptible degree from the adjacent specimens. But it does not at all follow because these intermediate forms have been found to exist, that they are the very stages that were passed through in the course of evolution. Counter evidence exists in abundance, not only of the appearance of considerable sports, but of their remarkable stability in hereditary transmission.

Again, Galton not only believed in the existence of both blended and alternative inheritance, but he recognized .the im-

2 *L. c.*, p. 30.
3 *L. c.*, p. 32.

portance of the latter in connection with the survival of new races.   Thus he writes:[4]

The quadroon child of the mulatto and the white has a quarter tint; some of the children may be altogether darker or lighter than the rest, but they are not piebald.[5] Skin-color is therefore a good example of what I call blended inheritance. . . .

Next as regards heritages that come altogether from one progenitor to the exclusion of the rest. Eye-color is a fairly good illustration of this. . . .

There are probably no heritages that perfectly blend or that absolutely exclude one another, but all heritages have a tendency in one or the other direction, and the tendency is often a very strong one.

On the following page Galton remarks that

A peculiar interest attaches itself to mutually exclusive heritages, owing to the aid they must afford to the establishment of incipient races.

He thus recognizes the invalidity of Darwin's objection to "single variations" as a factor in evolution, namely, that they would certainly be swamped by crossing with the general population.

It would, therefore, appear that in his recognition of continuity as well as discontinuity both in variation and heredity, Galton was in advance of his time, and more in accord with some of the current views.   R. RUGGLES GATES

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REPULSION IN MICE

IN the February number of the AMERICAN NATURALIST Dr. C. Little criticizes the results of my mouse-breeding experiments which I published in the *Zeitschrift für Induktive Abstammungs- und Vererbungs-lehre* Bd. VI, Heft 3. The chief point, on which he disagrees with me, is the interpretation of the results I obtained in breeding black and albino mice together.

The fact is, that in my paper on mice, I overlooked a serious error. In three sentences on page 126, relating to test matings of albinos, the words "black" and "agouti" changed places. As printed in the paper these sentences run:

Without exception they have given *black* or equal numbers of *black* and albino young, depending upon the purity of the black used. But never has one of these albinos produced a single *agouti* young in a mating with black. Counting together the colored young of such families I get 89 *black* young.

4 *L. c.*, p. 12.

5 Cases of piebaldism in such crosses are of course now well-known.

These errors were corrected in an ''errata'' in Band VI, heft 5, which Dr. Little unhappily did not find. The sentences should read:

Without exception they have given *agouti,* or equal numbers of *agouti* and albino young, depending upon the purity of the black used. But never has one of these albinos produced a single *black* young in a mating with black. Counting together the colored young of such families I get 89 *agouti* young.

Professor Punnett was so kind as to draw my attention to these mistakes. They were corrected in the reprints sent out.

The facts were simply these: Albinos were bred of two sorts, with and without G (the gene which agoutis have more than blacks). These albinos can only be distinguished by test-mating them to blacks. The albinos with G (aG) give agouti young, if mated to black (Ag), the ag albinos give black young from such a mating. In one series, some agoutis were produced, which were heterozygous for A as well as for G ($AaGg$). Ordinarily, such agoutis, when mated inter se, produce 9 agouti (1 $AAGG$, 2 $AAGg$, 2 $AaGG$, 4 $AaGg$), 3 black (1 $aaGG$, 2 $aaGg$) and 4 albinos (1 $aaGG$, 2 $aaGg$, 1 $aagg$) in every sixteen. Mated to albinos without G (ag) the ordinary $AaGg$ animals give four kinds of young, agoutis ($AaGg$), blacks ($Aagg$) and two kinds of albinos ($aaGg$) and ($aagg$) in equal numbers.

Now these particular $AaGg$ animals did not produce four kinds of gametes, as expected, namely, AG, Ag, aG and ag, but only two kinds, Ag and aG. Thirty one agoutis were test-mated to $aagg$ albinos. These test matings gave 181 young, of which 94 were black ($Aagg$) and 87 albino ($aaGg$). No agoutis were produced.

As a further proof, the result of breeding these agoutis inter se can be adduced. These matings gave 73 agouti ($AaGg$), 37 black ($AAgg$) and 32 albinos ($aaGG$). Of these 32 albinos, thirteen were tested by mating them to blacks. If one of them should have lacked G, it would have given black young. But no black young were produced. Some young were albino (when the black parent was heterozygous for A), but all the colored young were agouti (89 in all).

This, I hope, will make it perfectly clear, that in this series we have been dealing with a case of repulsion between the genes A and G.   A. L. HAGEDOORN

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THE OSTEOLOGY OF A DOUBLE–HEADED CALF

THROUGH the kindness of Mr. Charles O. Reed, taxidermist, of Fairmont, W. Va., the writer received the skulls and anterior cervical vertebræ of a double-headed calf which seemed of sufficient interest to warrant a brief description.

According to Mr. Reed the calf's mother was a four-year-old, thoroughbred Herford, living at Grafton, W. Va., owner not mentioned.

At her first labor this cow gave birth to twins, supposedly normal, though it was not so stated. The second calf was "slightly deformed," but in what way Reed did not know. The third labor produced the double-headed calf in question, which was of unusual size, and was killed in parturition. According to Reed "This calf would have lived if it could have been brought through O. K." He dissected it and found the "alimentary canal, blood vessels and trachea normal."

The bones in the occipital region are slightly broken, probably done in disarticulating the skulls from the neck; and in the left skull the left premaxilla was lost and was replaced by a roughly carved piece of wood for the sake of symmetry.

In macerating the skulls, for the purpose of removing all the flesh, many of the loose sutures separated, and in gluing the bones together again it was not always possible to completely close the sutures.

As may be seen in the figures there is a considerable though not very great difference in the size of the skulls, the right being the larger. They were detached from the cervical vertebræ when received, but the photographs show their approximate position in relation to the neck and to each other.

Each skull is twisted and bent away from the other, the bend being most marked just cephalad to the orbits. The left skull is the more distorted.

The articulation of the skulls with the fused atlas was so crude that Reed, who had seen the skulls before disarticulation, had to be appealed to to decide which skull was right and which was left.

Fig. 1 is a photograph of the dorsal aspect of the skulls and the first three cervical vertebræ. The distortion of the two skulls is of about the same character but is, as noted above, more marked in the left skull.

The parietal (p) is normal. The posterior regions of the frontals (f) are normal, but their anterior ends are bent laterally,

which causes a slight curvature in the sagittal suture. It is in the
region of the lachrymals (1) that the distortion is most marked,
so that the lachrymal on the convex side of the bend, especially

FIG. 1. DORSAL VIEWS OF THE TWO SKULLS AND OF THE FIRST THREE CERVICAL
VERTEBRÆ. MANDIBLES IN POSITION.

a, atlas; *ax*, axis; *e*, extra bone between maxilla and premaxilla; *f*, frontal;
l, lachrymal; *m*, malar; *mx*, maxilla; *n*, nasal; *o*, occipital; *p*, parietal; *pm*,
premaxilla.

in the left skull, is much longer than that on the opposite side;
the same is true of the malars (*m*), of the maxillaries (*mx*), and,
to a less degree, of the premaxillæ (*pm*). The nasals (*n*) are also
unsymmetrical, but do not differ much in size; they are simply,
as a pair, pushed to the side.

Fig. 2. The ventral aspect of the skull shows even greater ab-
normalities than the dorsal. The occipital (*o*), as noted above,
was somewhat injured by the person who disarticulated the skulls
from the neck, but it is quite unsymmetrical, especially in its
exoccipital region. In the left skull (right in this figure) all the
other bones seen in this aspect are bent, but in the other skull
most of the bones are comparatively straight.

In the right skull a suture in front of the teeth separates off an
extra bone (*e*) on each side, between the maxilla and the pre-
maxilla, that of the right side being much the larger. In the left
skull these extra bones are not present though a partial suture,

extending about half way through the left maxilla, is visible in this view of the skull.

FIG. 2.   VENTRAL VIEWS OF THE SKULLS AND THE FIRST TWO CERVICAL VERTEBRÆ.   MANDIBLES REMOVED.

Fig. 3 shows the curious distortion of the mandibles, which seem to be bent in more or less the same direction. In the right mandible the left half has four incisor teeth, the right half has three. In the left mandible the right half has four teeth, the left half has three, though one tooth is missing from each half.

As noted above, the skulls, when received, were disconnected from the vertebræ; but the latter, three in number, were strung together on a small piece of rope and presumably were the first three cervicals; they are shown in a dorsal view in Fig. 1, ventral view in Fig. 2, and anterior view in Fig. 3. The first of these is presumably a compound atlas (*a*) since it articulates with each of the skulls, though in a very crude way. It consists of eight loosely united elements which became completely separated in cleaning and had to be glued together again. In the dorsal view, Fig. 1, is seen a small, irregular bone from which radiate three somewhat symmetrical bones, the largest lying in the median plane between the bases of the skulls. This larger

bone is pierced by two large foramina; each of the other two bones shows in this view a foramen which branches and opens both on the antero-median and the postero-lateral surfaces. The

FIG. 3. DORSAL VIEWS OF THE MANDIBLES AND ANTERIOR VIEWS OF THE FIRST THREE CERVICAL VERTEBRÆ.

ventral view, Fig. 2, shows a very irregular group of bones, the smallest of which is for articulation with the following vertebra.

The second vertebra (*ax*), supposedly the axis, exhibits no indication of an odontoid process and articulates in a very crude way with the preceding bone. Its dorsal spine is rather elongated in an antero-posterior direction, but otherwise it bears no closer resemblance to an axis than to any other cervical vertebra. Its centrum was so loosely fused with the arch on either side it became detached in cleaning and had to be glued in place.

The third vertebra exhibits no peculiarities that warrant description.

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